Working Memory for Temporal and Nontemporal Events in Monkeys

Yoshio Sakurai[1]

Department of Psychology, Graduate School of Letters, Kyoto University, Kyoto 606-8501, Japan

This is the first report that introduces appropriate behavioral tasks for monkeys for investigations of working memory for temporal and nontemporal events. Using several behavioral tests, the study also shows how temporal information is coded during retention intervals in the tasks. Each of three monkeys was trained with two working memory tasks: delayed matching-to-sample of stimulus duration (DMS-D) and delayed matching-to-sample of stimulus color (DMS-C). The two tasks employed an identical apparatus and responses and differed only in the temporal and nontemporal attribute of the stimuli to be retained for correct performance. When a retention interval between the sample and comparison stimuli was prolonged, the monkeys made more incorrect responses to short samples in the DMS-C task, suggesting "trace decay" of memory for short stimuli. However, the same monkeys showed no such increase in incorrect responses to short samples in the DMS-D task, suggesting active coding of temporal information, that is, the length of stimulus duration, during the retention interval. When variable lengths of samples were presented with a fixed retention interval, the monkeys made more incorrect responses when length differences between short and long samples were small in the DMS-D task, but not in the DMS-C task. This suggests that the codes of working memory retained in the DMS-D task were not absolute (analogical) but rather were relative (categorical) and related to differences in the duration of the samples.

The neuronal coding of memory for temporal events remains unknown (Sakurai 1999a), though memorizing a presented stimulus inevitably requires coding of not only its color and shape but also its temporal duration. One strategy used to investigate the neuronal coding of temporal information is multiple-task comparisons (Sakurai 1996, 1999b) of neuronal activities; that is, recording and comparing neuronal activities when an animal is performing multiple tasks, one requiring memory for temporal events and the other requiring memory for nontemporal events.

Although working memory has been widely studied in neuroscience (e.g., Funahashi 2001; Wickelgren 2001), little research has focused on working memory for temporal information. The present study was designed to focus on working memory for temporal information that is inherent to external stimuli. This study introduces, for the first time, appropriate multiple behavioral tasks to investigate working memory for temporal and nontemporal events in monkeys and shows how temporal information is coded in the tasks by several behavioral tests.

Working memory for temporal events has been examined using pigeons and rats, as reviewed by Santi et al. (1995, 1998). However, the previous studies' findings suggesting features of memory codes for temporal events were not consistent with each other. The reason for the inconsistency might be that the behavioral tasks employed in the studies were not appropriate to investigate codes of temporal samples, as Santi et al. (1998) indicated. For instance, the behavioral tasks did not rule out the possibility that the animals' responding was controlled not by the temporal duration of stimuli to be coded during retention intervals but by the total trial and/or intertrial intervals (e.g., Raslear et al. 1992). In addition, the tasks in these studies included several types of conditional discrimination tasks, in which a sample stimulus indicated one comparison stimulus to which the animal had to respond and the rewards were delivered to just one comparison stimulus or one go/no-go response. This means that the animal in such tasks could decide what comparison stimulus to choose or what response to make immediately when the sample stimulus was presented and does not necessarily need to retain the sample stimulus during retention intervals. Thus, those procedures allowed the possibility of "prospective coding," that is, coding and expectancy of the forthcoming correct comparison and/or response (Grant and Kelly 1996), as opposed to "retrospective coding," that is, coding and retention of the previously presented sample. Precisely controlled working memory tasks are therefore required for temporal events, in which only the temporal length of the presented sample is a cue for correct performance and is retrospectively coded and retained during retention intervals.

Such controlled multiple behavioral tasks were used in the present study to investigate working memory for tem-

[1]Corresponding author.
E-MAIL sakurai@psy.bun.kyoto-u.ac.jp; FAX 81-75-753-2848.
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poral and nontemporal events. In the tasks, total trial and intertrial intervals cannot be cues for correct performance, and the possibility of prospective coding is ruled out.

Preliminary findings regarding behavioral analysis of these tasks (Sakurai 1999c) and the prefrontal neuronal activities of monkeys during performance of the tasks (Sakurai et al. 2001) have been reported briefly elsewhere.

RESULTS

Tasks and Acquisition

Three rhesus monkeys were used. Each monkey was trained with two behavioral tasks (Fig. 1). The task to assess working memory for temporal events was delayed matching-to-sample of duration (DMS-D). When the monkey pressed a lever, a small fixation spot appeared on a computer display in front of the monkey and then large green squares appeared twice in succession with a 3-sec retention interval between them. The first square was a sample stimulus and the second was a comparison stimulus. They were presented for 0.5 or 2.0 sec. If the sample and comparison durations were different (nonmatch), a go response (releasing the lever when the fixation spot shrank) was correct. If their durations were identical (match), a no-go response (releasing the lever when the fixation spot returned to the normal state) was correct. A liquid reward was given for both correct go and correct no-go responses.

The task to assess working memory for nontemporal events was delayed matching-to-sample of color (DMS-C). The sequence of stimuli and responses were the same as in the DMS-D task, except that the sample and comparison stimuli were not green but red or blue. When the sample and comparison colors were different (nonmatch), go responses were correct and rewarded. When their colors were identical (match), no-go responses were correct and rewarded. Durations (0.5 or 2.0 sec) of samples and comparisons were not relevant to correct performance.

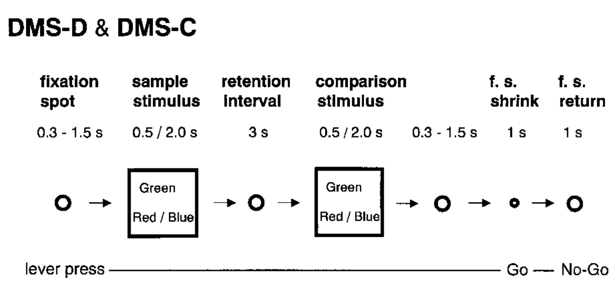

Figure 1 The sequences of stimuli and responses in the DMS-D and DMS-C tasks. The first square is a sample stimulus, and the second square is a comparison stimulus. Releasing the lever when the fixation spot shrinks was designated a "Go" response, and releasing it when the fixation spot returns was a "No-Go." The sequences in the DMS-D and DMS-C tasks were identical except that sample and comparison stimuli were always green in the DMS-D task but red or blue in the DMS-C task.

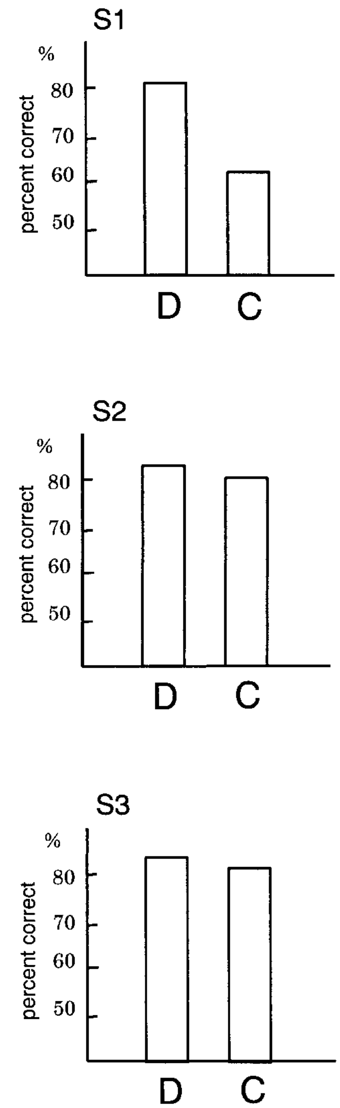

Figure 2 Median correct responses for all monkeys in the DMS-D (D) and DMS-C (C) tasks successively given on a given day. The data were obtained from the last training sessions (320 trials per task) of the tasks after ~150 days of training.

Acquisition accuracy was calculated with a ratio of correct/total trials in a session of approximately 400 rewarded trials in each task, and the criterion for good performance was more than 80% correct trials in a session. Of the three monkeys, S2 and S3 achieved the criterion performance after 110 and 90 days of training in the DMS-D task and after 35 and 50 days of training in the DMS-C task, respectively. They finally showed good performance in both tasks given successively on one day after approximately 150 days of training in total (Fig. 2). One monkey (S1) achieved the criterion performance after 110 days of training in the DMS-D task and after 70 days of training in the DMS-C task. However, that monkey showed good performance in only the DMS-D task when the two tasks were given successively on one day even after 250 days of training in total. The data in the following behavioral tests, therefore, were obtained from all three monkeys (S1, S2, and S3) for performance in the DMS-D task and from only two monkeys (S2 and S3) for performance in the DMS-C task.

Retention Test

After completion of training, the monkeys were given a retention test in which retention intervals between sample and comparison stimuli in the tasks were manipulated. Equal numbers of trials with 1-sec, 3-sec, 5-sec and 7-sec retention intervals were randomly presented within a session of 320 trials.

Figure 3 shows median percent correct responses during the retention test in the DMS-D task. When the retention intervals were longer than 3 sec, which was the original retention interval in the training, total correct responses significantly decreased in all monkeys (X^2 = 20.14 ~33.02, $df = 3$, $P < .001$). Figure 3 also shows median percent correct responses when the samples to be retained in retention intervals were short (0.5 sec) and long (2.0 sec). The different lengths of sample had no effect on correct performance in any of the monkeys.

Figure 4 shows such correct performance changes in the retention test in the DMS-C task. As described above in the Tasks and Acquisition section, the data for the DMS-C task were obtained from two monkeys (S2 and S3). As in the DMS-D task, the total number of correct responses decreased significantly in both monkeys when the retention intervals were prolonged (X^2 = 22.05 ~38.11, $df = 3$, $P < .001$). However, the different lengths of sample had significant effects on correct performance, with performance to the short samples (0.5 sec) being worse than to long samples (2.0 sec) (X^2 = 6.36 ~10.17, $df = 2$, $P < .05$).

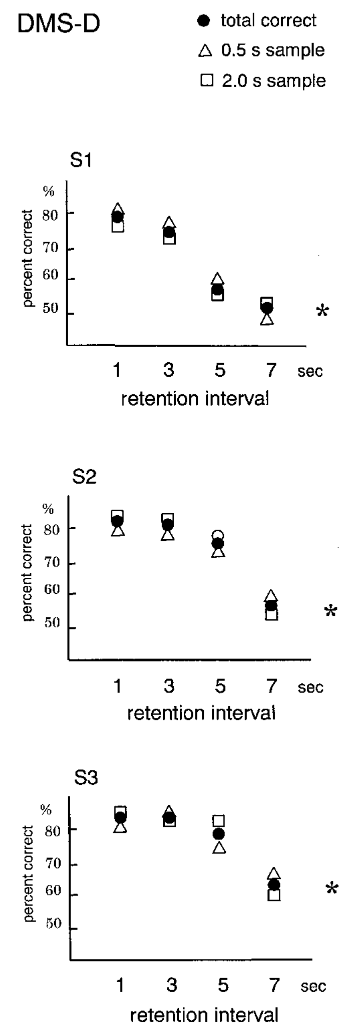

Figure 3 Median correct responses for all monkeys as a function of retention intervals of the retention test in the DMS-D task. Besides total correct responses (●), correct responses for short (△) and long (□) samples are shown separately. The asterisk at the far right in each panel indicates significant effects of changes of retention interval on total correct responses.

Discrimination Tests

Following the retention test, the monkeys were given discrimination tests in which lengths of sample and comparison stimuli were manipulated with a fixed 1-sec retention interval. In discrimination test 1, the short stimulus (0.5) was not manipulated and the long stimulus (2.0 sec) was changed to 2.5 sec, 1.5 sec, and 1.0 sec in a session of 320 trials. The monkeys were trained in both DMS-D and DMS-C tasks with the 2.5-sec long stimulus for 7 d, and then with the 1.5-sec long stimulus for 7 d, and finally with the 1.0-sec long stimulus for 7 d. In discrimination test 2, the long stimulus was fixed to the original length (2.0 sec), and the short stimulus (0.5 sec) was changed to 0.25 sec, 1.0 sec, and 1.5 sec. As in the discrimination test 1, the monkeys were trained in both DMS-D and DMS-C tasks for 21 d, in which the changed three short stimuli were used for 7 d each.

Figure 5 shows median percent correct responses in the period of the discrimination test 1 in which the long stimuli were manipulated in the DMS-D task. All monkeys performed well when the long stimulus was 2.5 sec, but their correct responses decreased with the 1.5-sec long stimulus and were at almost chance levels with the 1.0-sec long stimulus. The effects of changes of the long stimuli on correct performance were significant in all monkeys (X^2 = 19.31 ~20.92, $df = 2$, $P < .001$). In the DMS-C task (Fig. 6), however, the changes of the long stimuli had small significant effects on correct performance only during the first few days of the 7-d period in all monkeys (X^2 = 6.36 ~7.94, $df = 2$, $P < .05$). The monkeys performed well in the latter part of the 7-d period.

Figure 7 shows median percent correct responses in

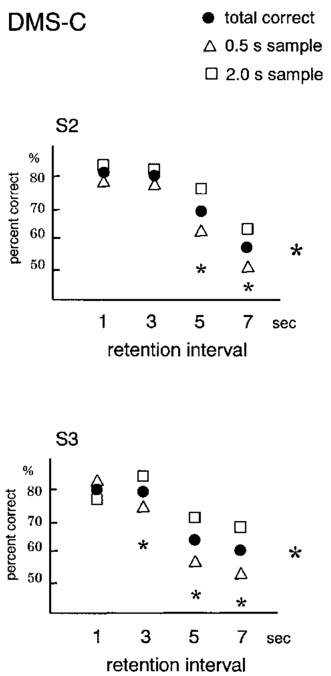

Figure 4 Median correct responses for monkeys S2 and S3 as a function of retention intervals of the retention test in the DMS-C task. All parameters and symbols are as in Fig. 3. The small asterisk in each panel indicates a significant difference of correct responses between the short and long samples.

the period of the discrimination test 2 in which the short stimuli were manipulated in the DMS-D task. All monkeys performed well when the short stimulus was 0.25 sec, but their correct responses decreased with the 1.0-sec short stimulus and were at almost chance levels with the 1.5-sec short stimulus. The changes of short stimuli had significant effects on correct performance in all monkeys (X^2 = 21.55 ~27.28, *df* = 2, *P* < .001). In the DMS-C task (Fig. 8), however, changes of the short stimuli had no effect on correct performance except during the first 2 d of the period in monkey S2 (X^2 = 6.02 ~9.33, *df* = 2, *P* < .05). All monkeys performed well throughout almost the entire period with the changed short stimuli.

DISCUSSION

This study utilized multiple tasks to assess working memory for temporal and nontemporal samples and showed that monkeys could be trained to perform both tasks well. In the task with temporal samples, delayed matching-to-sample of stimulus durations, total trial and/or intertrial intervals could not serve as cues for correct performance. The only strategy for the monkeys to perform correctly was retrospective coding; that is, retaining temporal lengths of the samples during the retention intervals, and then comparing them with the lengths of comparison stimuli. Prospective coding, that is, not retention of the samples but representation of upcoming meaningful stimuli to respond to, could do nothing for correct performance, because both go responses for nonmatch stimuli and no-go responses for match stimuli were meaningful and rewarded, and the monkeys could not predict, during the retention intervals, which of the stimuli was upcoming as a comparison stimulus. Moreover, not only contingencies of reward for go and no-go responses but also motor activities for go and no-go responses were symmetrical and equally controlled in nonmatch and match trials, because the monkeys needed to perform the same motor activity (releasing the lever) for both go responses to nonmatch stimuli and no-go responses to match stimuli.

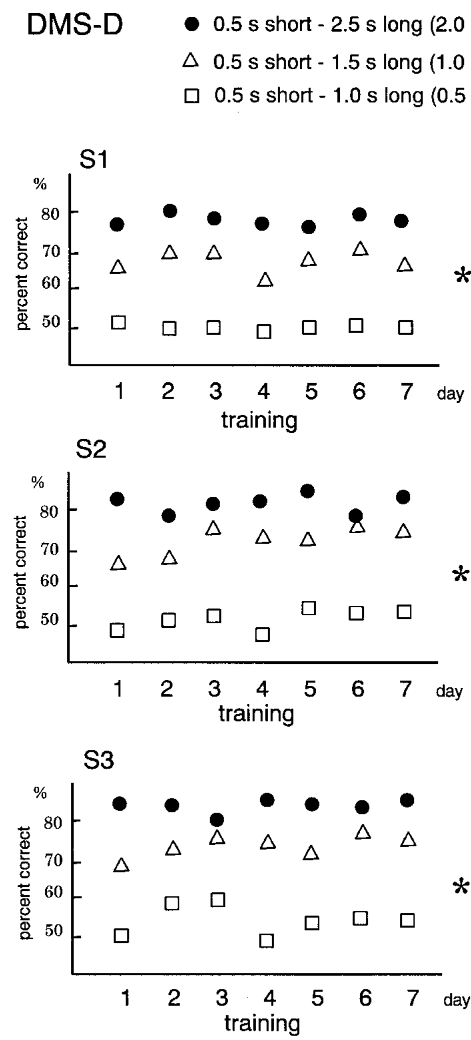

Figure 5 Median correct responses for all monkeys in the period of the discrimination test 1 in the DMS-D task. Long stimuli were manipulated (2.5 sec ●, 1.5 sec △, and 1.0 sec □), whereas short stimuli were usual and fixed (0.5 sec). The seconds in the parentheses at the top right indicate the time differences between the short and long stimuli. The asterisk at the far right in each panel indicates significant effects of the changes of long stimuli on correct responses throughout the test period.

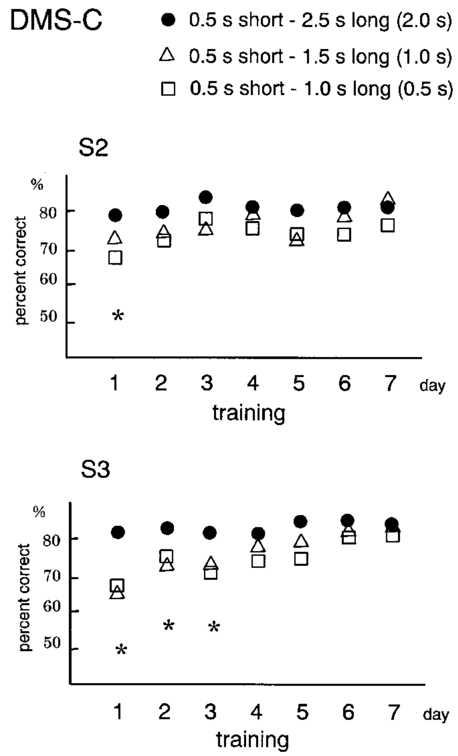

Figure 6 Median correct responses for monkeys S2 and S3 in the period of the discrimination test 1 in the DMS-C task. All parameters and symbols are as in Fig. 5. The small asterisk in each panel indicates a significant difference of correct responses among the different long stimuli within each day in the test period.

Previous behavioral studies which investigated working memory for temporal samples in animals used pigeons and rats (Spetch and Wilkie 1983; Grant and Spetch 1991; Santi et al. 1993, 1995, 1998). The tasks in those studies were conditional discrimination tasks; lengths of stimuli and intertrial intervals were not separately controlled, and/or motor activity for correct responses and reward delivery were asymmetrical (as noted earlier herein). As a consequence of those methodological problems, there remained the possibility that the animals' responding might be controlled by total trial and/or intertrial intervals and by prospective coding of forthcoming meaningful stimuli or responses, not by to-be-coded durations of sample stimuli and retrospective coding of the samples (Santi et al. 1998). Therefore, it can be said that the present study is the first to use a precisely controlled working memory task for investigation of the coding of temporal samples in animals.

In the retention test, the monkeys made more incorrect responses when the retention intervals between the sample and comparison stimuli were prolonged, in both the DMS-D and DMS-C tasks. This is a retention interval-dependent decline of working memory, indicating that memory codes of the samples were retained during the retention intervals. The monkeys performing the retention test in the DMS-C task showed more incorrect responses to the short samples. This means that there was "trace decay" of memory codes for briefly presented samples (e.g., Roberts 1972; Herzog et al. 1977), suggesting that the samples were coded retrospectively and longer samples were represented more clearly in the memory code. This trace decay of memory codes in the DMS-C task also suggests that the temporal lengths of samples were not informative in the DMS-C task and the monkeys did not actively code but just passively received the temporal lengths of the samples. The same monkeys, however, showed no increase in incorrect responses to the short samples in the DMS-D task, indicating that trace decay of memory codes for the short samples did not occur. This finding suggests that the temporal lengths of samples were informative in the DMS-D task and the monkeys actively coded the temporal information and retained that code during the retention intervals. The DMS-D task, therefore, is surely appropriate to investigate working memory for temporal information.

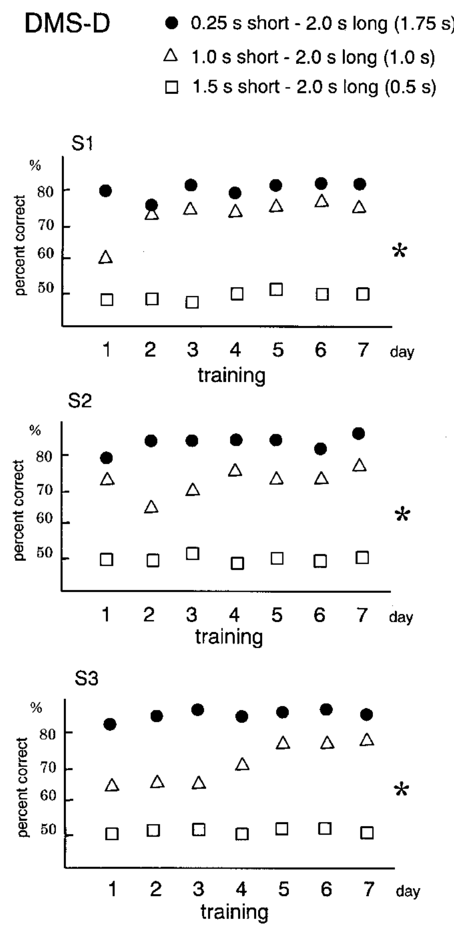

Figure 7 Median correct responses for all monkeys in the period of the discrimination test 2 in the DMS-D task. Short stimuli were manipulated (0.25 sec ●, 1.0 sec △, and 1.5 sec □) whereas long stimuli were usual and fixed (2.0 sec). All parameters and symbols are as in Fig. 5.

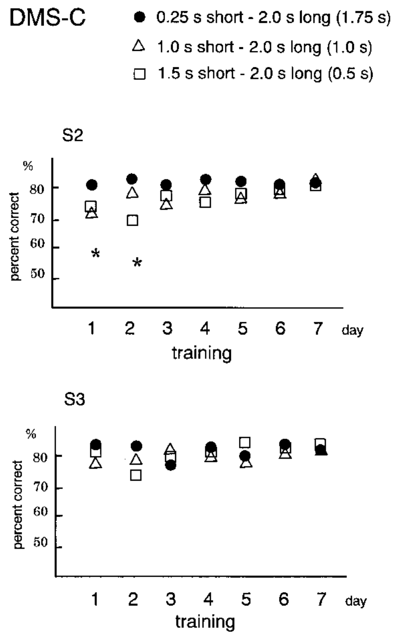

Figure 8 Median correct responses for monkeys S2 and S3 in the period of the discrimination test 2 in the DMS-C task. All parameters and symbols are as in Fig. 7.

A phenomenon known as the "choose-short effect" has arisen in behavioral studies of working memory for temporal events in pigeons (Spetch and Wilkie 1982; Spetch 1987; Spetch and Rusak 1989). As the retention interval increased in those studies, the pigeons showed an increasing tendency to peck the comparison stimulus corresponding to the short-duration sample, though the short- and long-duration samples were equally presented. A model to explain such biased choosing of short samples is called the "subjective shortening" model (Spetch and Wilkie 1983). The model assumes that the pigeons retain temporal information in a retrospective fashion and that the subjective duration of the sample decreases during the retention interval. However, the retention test used in the present study showed that the monkeys retaining temporal information of samples in a retrospective fashion had no choose-short effect; that is, they showed no tendency for more responses corresponding to the short samples even when the retention intervals were prolonged. Therefore, the subjective shortening model of working memory for temporal events cannot be generalized for all species and tasks, and should be more closely examined with appropriately controlled behavioral tasks.

In the discrimination tests, variable lengths of samples and comparisons were presented with the retention interval fixed. Such changes of stimulus lengths had strong effects on the monkeys' performance only in the DMS-D task. The monkeys showed poorer performance when the long stimulus (2.0 sec) was changed to the shorter ones (1.5 sec and 1.0 sec in discrimination test 1) and the short stimulus (0.5 sec) was changed to the longer ones (1.0 sec and 1.5 sec in discrimination test 2). The same monkeys, however, performed well when the long stimulus was changed to the longer one (2.5 sec in discrimination test 1) and the short stimulus was changed to the shorter one (0.25 sec in discrimination test 2). These results indicate that not the lengths themselves but the relative differences in length between the short and the long stimuli affected the monkeys' performance, suggesting that the temporal information the monkeys retained in the DMS-D task was not absolute (analogical, i.e., exact lengths of the stimuli, 0.5 sec and 2.0 sec), but rather was relative (categorical, i.e., relative differences of longer and shorter durations).

Studies of working memory for temporal events in pigeons and rats have examined the relations among different coding fashions; that is, categorical, analogical, retrospective, and prospective coding (Santi et al. 1993). The subjective shortening model described above proposes that event durations are coded in an analogical and retrospective fashion (Spetch and Sinha 1989). This analogical-retrospective relation in coding has been confirmed by other behavioral studies (e.g., Wilkie and Willson 1990), and a categorical-prospective relation was also proposed (Santi et al. 1993). However, the discrimination tests used in the present study showed that the monkeys retained temporal information in a categorical fashion; that is, they remembered relative differences of the short and long samples. Therefore, the present results suggest a new categorical-retrospective relation in the coding of temporal events. Relationships among the several coding fashions for temporal information should be examined again with appropriately controlled behavioral tasks.

The multiple tasks in the present study were not strictly parallel to each other. In the DMS-D task, the monkeys had to attend to the duration of two stimuli in the same color, whereas in the DMS-C task they had to not only attend to the color of two stimuli but also ignore or suppress the changes of duration of the stimuli. Such an additional load might have caused the poor performance in monkey S1 in the DMS-C task when the two tasks were carried out in one day (Fig. 2); that is, the monkey might have failed to ignore or suppress differences of stimulus duration no longer unimportant in the DMS-C task. This biased load between the DMS-C and DMS-D tasks, however, is not likely to have affected the results in the retention and discrimination tests. In the retention test (Figs. 3, 4), the total correct performances for all retention intervals were not different between the DMS-C and DMS-D tasks. Moreover, the result that the short samples were more easily forgotten than the long samples when the retention intervals were prolonged cannot be explained by the additional load in the DMS-C task. In the discrimination tests (Figs. 5–8), the correct performances when the short–long differences were large were not worse in the DMS-C task than those in the DMS-D task. It is concluded that the additional load in the DMS-C task cannot explain the observation that the small differences between short and long samples resulted in poor performances in the DMS-D task but not in the DMS-C task.

MATERIALS AND METHODS

Animals

The subjects were three female rhesus monkeys (*Macaca mulatta*) weighing 5.0, 5.0, and 5.6 kg during the experiment. The monkeys were housed in individual cages and were normally deprived of water in their home cages. They were able to obtain their daily requirement of water in the laboratory in the form of supplement water (sports drink) as reward during training or testing sessions. As necessary, they received supplemental water, sweet potatoes, and fruit in their home cages to keep their weight stable. Water was given ad lib more than one day a week in the cages. To maintain the health of the monkeys, body weight and daily water intake were monitored, and staff veterinarians included the monkeys in their routine round of health checks. All experiments were performed in accordance with NIH's "Guidelines for care and use of laboratory animals" (1985) and Kyoto University Primate Research Institute's "Guide for care and use of laboratory primates" (1996).

Apparatus

In a dim, sound-attenuated, and electrically shielded room, the monkey sat in a primate chair facing a 17-inch color display monitor. A response lever was set just in front of the monkey's arms in the chair. A system with a CCD camera was used for monitoring eye position and movement. The task events were controlled by a personal computer system.

Tasks

The sequences of events in the DMS-D and DMS-C tasks are illustrated in Figure 1. The monkey initiated each trial by pressing the lever. This turned on a white fixation spot (2°) on the center of the display. The monkey needed to continue pressing the lever to complete the trial. After a variable time interval (0.3–1.5 sec) from the fixation spot on, a sample stimulus (a square of 10°) appeared for 0.5 sec or 2.0 sec, then the fixation spot appeared for 3.0 sec (retention interval), and a comparison stimulus (a square of 10°) appeared for 0.5 sec or 2.0 sec. In the DMS-D task, the color of both the sample and comparison stimuli was green. In the DMS-C task, the sample and comparison stimuli were blue or red. Following the end of the comparison stimulus, the fixation spot appeared for a variable time interval (0.3–1.5 sec), then it shrank to 0.7° for 1.0 sec and returned to 2° for 1.0 sec. The monkey had to release the lever when the fixation spot shrank (go response) to get a reward on a nonmatch trial. The monkey had to release the lever when the fixation spot returned to 2° (no-go response) to get a reward on a match trial. To-be-compared attributes of sample and comparison stimuli for match/nonmatch judgments were their durations (0.5 sec and 2.0 sec) in the DMS-D task and their colors (red and blue) in the DMS-C task. The reward was a drop of 0.3 cc sports drink delivered on both correct go and correct no-go responses. If the monkey made incorrect go or no-go responses, 10 sec of time out was given, during which pressing the lever was invalid and the monkey could not start the next trial. In addition, any incorrect response was followed by a correction trial in which the same sample and comparison stimuli as in the preceding trial were presented and a correct response was required. No data were obtained from the correction trials. If the monkeys did not release the lever until the end of the period for a no-go response or released the lever by the start of the period for a go response, the trial was canceled and the monkey had to start it again by releasing and pressing the lever.

Training

The monkeys were trained about 800 rewarded trials/session in a day until they reached a criterion of better than 80% correct trials in a session. Each monkey was trained in the DMS-D task first to the criterion and then trained in the DMS-C task to the criterion. The monkeys were then trained in both tasks randomly presented in order on each day.

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REFERENCES

Funahashi, S. 2001. Neuronal mechanisms of executive control by the prefrontal cortex. *Neurosci. Res.* **39:** 147–165.

Grant, D.S. and Kelly, R. 1996. The roles of minimum wait time and sample discriminability in the coding of event duration in pigeons. *Learn. Motiv.* **27:** 243–259.

Grant, D.S. and Spetch, M.L. 1991. Pigeons' memory for event duration: Differences between choice and successive matching tasks. *Learn. Motiv.* **22:** 180–199.

Herzog., H.L., Grant, D.S., and Roberts, W.A. 1977. Effects of sample duration and spaced repetition upon delayed matching-to-sample in monkeys (*Macaca arctoides* and *Saimiri sciureus*). *Anim. Learn. Behav.* **5:** 347–354.

Raslear, T.G., Shurtleff, D., and Simon, L. 1992. Intertrial-interval effects on sensitivity (*A*') and response bias (*B*") in a temporal discrimination by rats. *J. Exp. Analy. Behav.* **58:** 527–535.

Roberts, W.A. 1972. Short-term memory in the pigeon: Effects of repetition and spacing. *J. Exp. Psychol.* **94:** 74–83.

Sakurai, Y. 1996. Hippocampal and neocortical cell assemblies encode memory processes for different types of stimuli in the rat. *J. Neurosci.* **16:** 2809–2819.

Sakurai, Y. 1999a. How do cell assemblies encode information in the brain? *Neurosci. Biobehav. Rev.* **23:** 785–796.

Sakurai, Y. 1999b. Elemental, configural, and sequential memory processes in the rat can be tested in a single situation in one day. *Psychobiol.* **27:** 486–490.

Sakurai, Y. 1999c. Behavioral analysis of delayed matching to samples of stimulus duration by rhesus monkeys. *Neurosci. Res.* Suppl. **23:** 255.

Sakurai, Y., Takahashi, S., and Inoue, M. 2001. Multi-neuronal activities related to short-term retention of stimulus duration in the monkey prefrontal cortex. *Neurosci. Res.* suppl. 25 (in press).

Santi, A., Bridson, S., and Ducharme, M.J. 1993. Memory codes for temporal and nontemporal samples in many-to-one matching by pigeons. *Anim. Learn. Behav.* **21:** 120–130.

Santi, A., Stanford, L., and Coyle, J. 1998. Pigeons' memory for event duration: Differences between visual and auditory signals. *Anim. Learn. Behav.* **26:** 163–171.

Santi, A., Weise, L., and Kuiper, D. 1995. Memory for event duration in rats. *Learn. Moti.* **26:** 83–100.

Spetch, M.L. 1987. Systematic errors in pigeons' memory for event duration: Interaction between training and test delay. *Anim. Learn. Behav.* **15:** -5.

Spetch, M.L. and Rusak, B. 1989. Pigeons' memory for event duration: Intertrial interval and delay effects. *Anim. Learn. Behav.* **17:** 147–156.

Spetch, M.L. and Sinha, S.S. 1989. Proactive effects in pigeons' memory for event durations: Evidence for analogical retention. *J. Exp. Psychol.: Anim. Behav. Proc.* **15:** 347–357.

Spetch, M.L. and Wilkie, D.M. 1982. A systematic bias in pigeons' memory for food and light durations. *Behav. Anal. Lett.* **2:** 267–274.

Spetch, M.L. and Wilkie, D.M. 1983. Subjective shortening: A model of pigeons' memory for event duration. *J. Exp. Psychol.: Anim. Behav. Proc.* **9:** 14–30.

Wickelgren, I. 2001. Neurobiology: Working memory helps the mind focus. *Science* **291:** 1684–1685.

Wilkie, D.M. and Willson, R.J. 1990. Discriminal distance analysis supports the hypothesis that pigeons retrospectively encode event duration. *Anim. Learn. Behav.* **18:** 124–132.

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